STATOCYTES OF THE WHEAT HAULM

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(WITH FOUR FIGURES)

The plant statocyte is a cell containing a body or bodies, the statoliths, free to move within it under the force of gravity (**1, 5**). In the mature wheat haulm, the statocytes are entirely confined to the "nodes"[1] or swellings of the leaf sheaths just above their attachment to the stem. Here they occupy more than half the total bulk, forming a definite and continuous tissue, which I have previously termed statenchyma (**5**).

Fig. 1 makes the anatomy in this region clear. The swollen leaf sheath is bordered within and without by an epidermis succeeded by a few layers of collenchyma of the type described by HABERLANDT as lamellar (**2**, p. 156). Between these layers the fibrovascular strands, consisting mainly of slightly lignified fibers, are arranged in an irregular ring, varied occasionally by smaller strands of similar fibers unaccompanied by, or surrounding a trace only of vascular tissue. The whole, or nearly the whole of the ground tissue is transformed into statenchyma, more highly differentiated than usual, since the statoliths are of two kinds. The more general type of statolith (the starch grain) is found in groups of cells occurring adaxially to the vascular strands. These sometimes form only one or two layers, but occasionally are more extensive, and even reach the internal collenchyma (fig. 1). All the other statocytes, composing by far the greater part of the ground tissue, contain crystal statoliths, and are best developed internally to, and on the flanks of the fibrovascular strands.

This position of the statenchyma within the vascular ring is unusual, although not without parallel.[2] A crystal statolith, however, is probably extremely rare, for, although expecting it, I have

[1] The term "node" is used throughout the paper in this sense.

[2] In 1911 I figured (**3**) the statocyte pith of *Hottonia palustris*, and since then other cases have become known to me of the conversion of the pith in whole or in part to statenchyma.

never discovered it elsewhere, notwithstanding careful search in more than a hundred plants, widely differing in habit and systematic position.

The crystal-containing statocytes are nearly twice as broad as they are long, that is, they are compressed in the axial plane. In shape they are irregularly cylindrical and hence circular in transverse section, while the longitudinal walls are generally more or less gabled (cf. fig. 3). The shape and arrangement of these cells thus allow easy extension of the tissue on bending of the node. The average diameter of the cells is about 55 μ, and the height about 30 μ. The walls are pitted, which is best seen in transverse sections showing the flat horizontal walls in surface view. Each contains a relatively large nucleus (about 18 μ diameter). In one case two nuclei were seen, although to what extent this is a general phenomenon in the wheat plant has not yet been determined (cf. **4**, note at end). The crystals usually occur singly in the cells, and when there are several this is probably due in some cases to fracture. They apparently belong to the tetragonal system (10 μ diameter), and occur as prisms, pyramids, spherical aggregates, combinations of these, or in less definite forms (fig. 4). Hydrochloric acid dissolves them at once, but they are unaffected by glacial acetic acid and various stains. From these facts their chemical composition is judged to be calcium oxalate.

The amylostatocytes decrease in size as they approach the vascular tissue, and are of much smaller average diameter than the crystal statocytes (fig. 2). Each possesses a nucleus (about 10 μ diameter), and numerous starch grains occupying about half the volume of the cell. The grains are simple, spherical, and about 5 μ in diameter. Movable crystals may also occur in these cells.

Search has been made for starch and crystals in other parts of the mature wheat plant. The latter occur in the pith of the stem, but are not free to move; and, except of course in the grain, only traces of imbedded starch have occasionally been found. Preliminary work on the seedling and young plant indicates that statolith starch exists throughout its life and appears in the same locality, that is, it is constant in time and space, while imbedded starch is neither. The latter naturally tends to disappear from all parts while the grain is filling, and it is therefore a fact to be noted that the statolith starch is unaffected by this drain on the stored food material, and therefore cannot be regarded as primarily nutritive in function.

Both DARWIN and HABERLANDT have referred to the "falling time" (**1**, p. 771), and "period of migration" (**2**, p. 598) of statoliths, but I am not aware of any work on the *rate* of travel other than my own, which is not yet published in full (**6**). The unique feature of the wheat plant in possessing two kinds of statoliths, together with its extreme economic importance, perhaps justify a separate statement at the present time. Experimental work has demonstrated the fact that the rate of travel of the crystal is much greater than that of the starch grain, for the latter falls at about 120 μ per hour, while the rate of the former is nearer 600 μ.

The rate of the starch grain approximates to that obtained for the movable starch grains in the inflorescence axis of *Lupinus*, and is probably very average, but 600 μ per hour is about three times as great as that of any statolith known to me.

The actual time taken for the crystal to travel from one side of the cell to the other is probably under 5 minutes, and the same period for the starch grain varies with the diameter of its statocyte, but averages about 15 minutes. In nature, however, since the statocyte could never be displaced more than 90° from the vertical, the statolith would never traverse the whole diameter of the cell, but some distance less than this, and hence would reach its new position in a period of time less than that stated.

If the impact of the falling body on the living protoplasm lining the cell is a means of perception by the plant of the direction of gravity (**1**, **2**), it is the latter period which is of biological importance. It then becomes interesting to note that this period is the shortest on record. The wheat is capable of bending at the nodes in order to bring the haulm into a vertical position should it be displaced; and it is an obvious saving of energy in the transmission of stimulus that these organs should be at the same time both sensory and motor, that is, capable of perceiving and also of acting upon the appropriate stimulus.

The recognition of the node as indeed a definite sense organ of gravity perception on the part of the wheat plant readily accounts for the presence of starch in this region when the ear is ripe, which otherwise seems difficult of explanation.

I would further suggest the possibility that in the course of evolution the wheat plant may be substituting a body, metabolically harmful, but heavier and therefore quicker and better as a

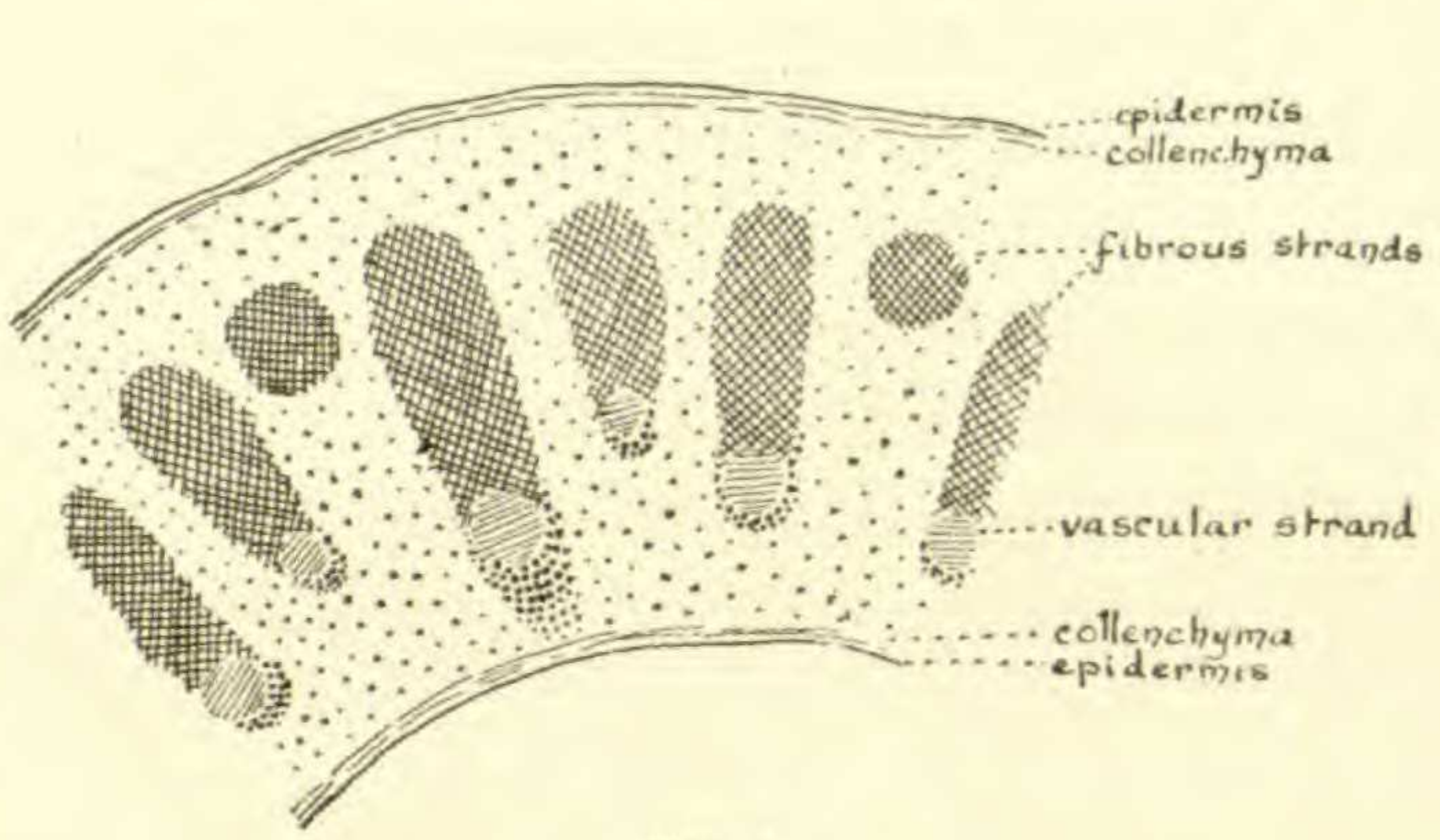

FIG. 1

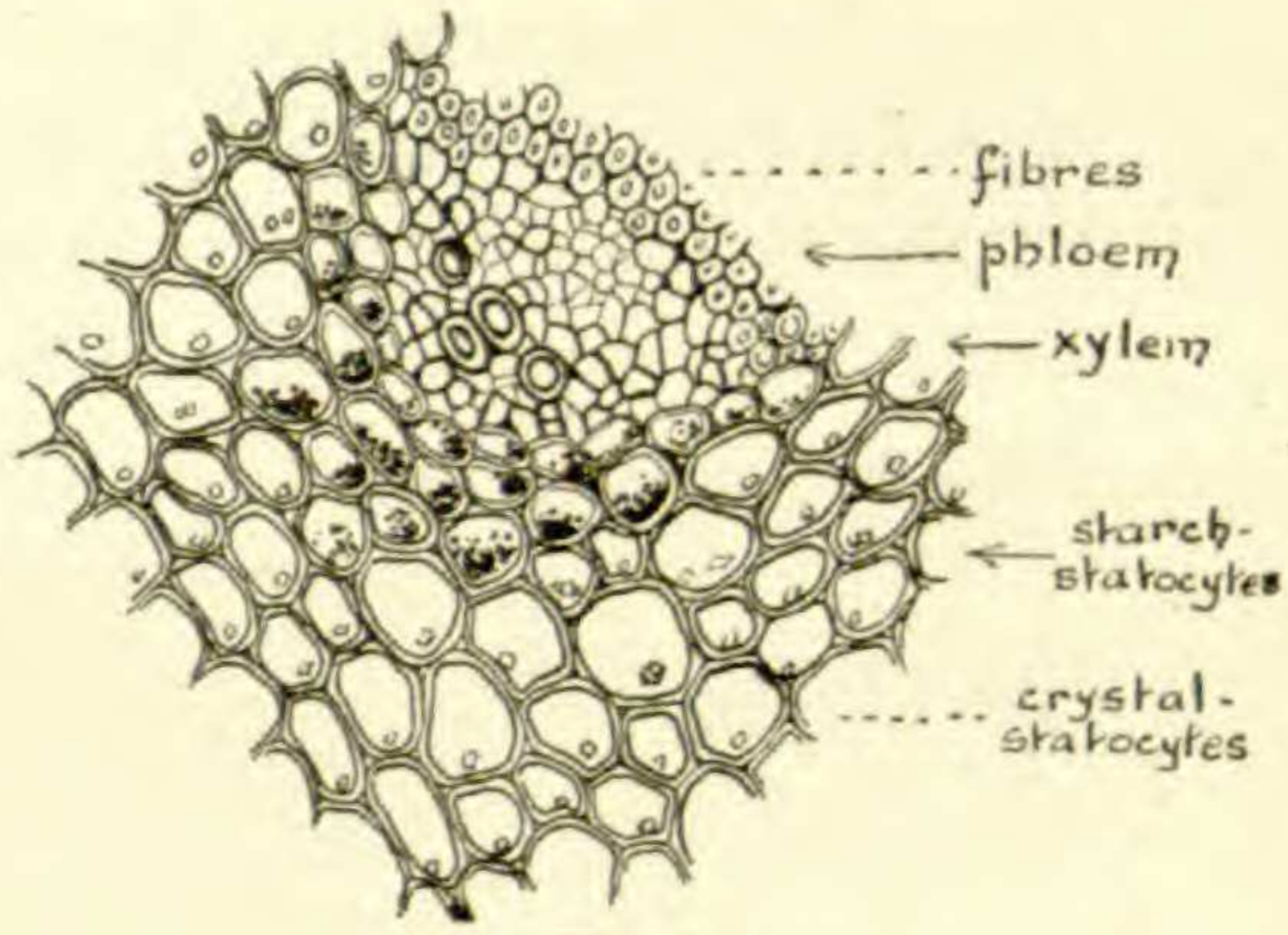

FIG. 2

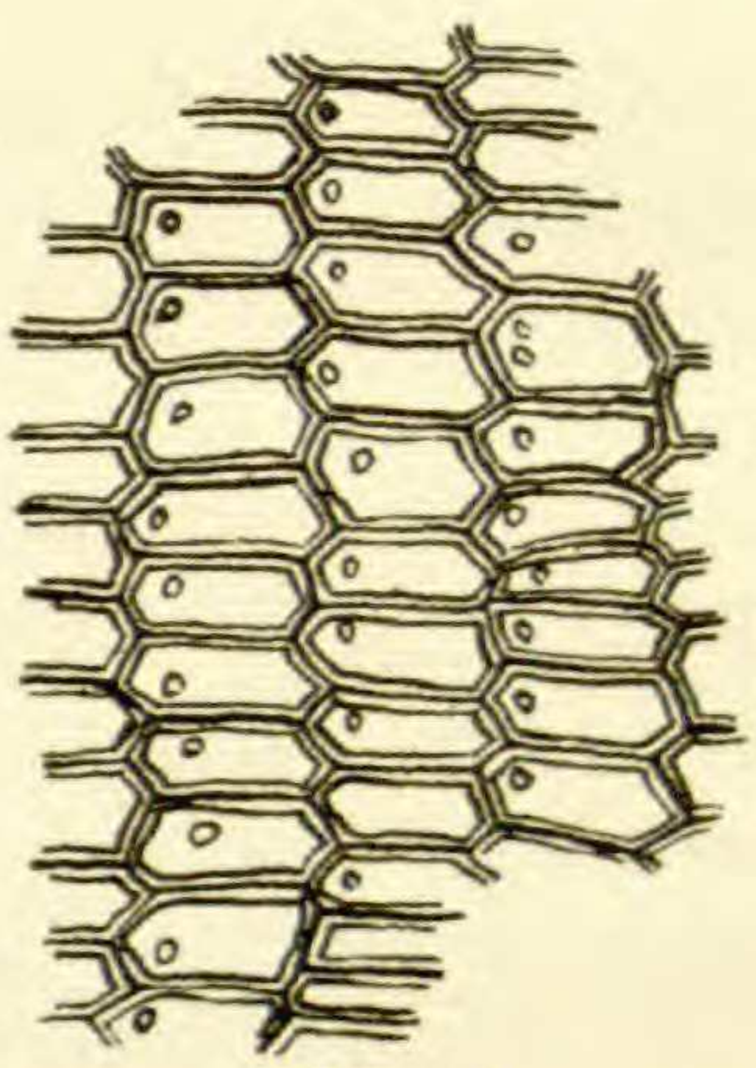

FIG. 3

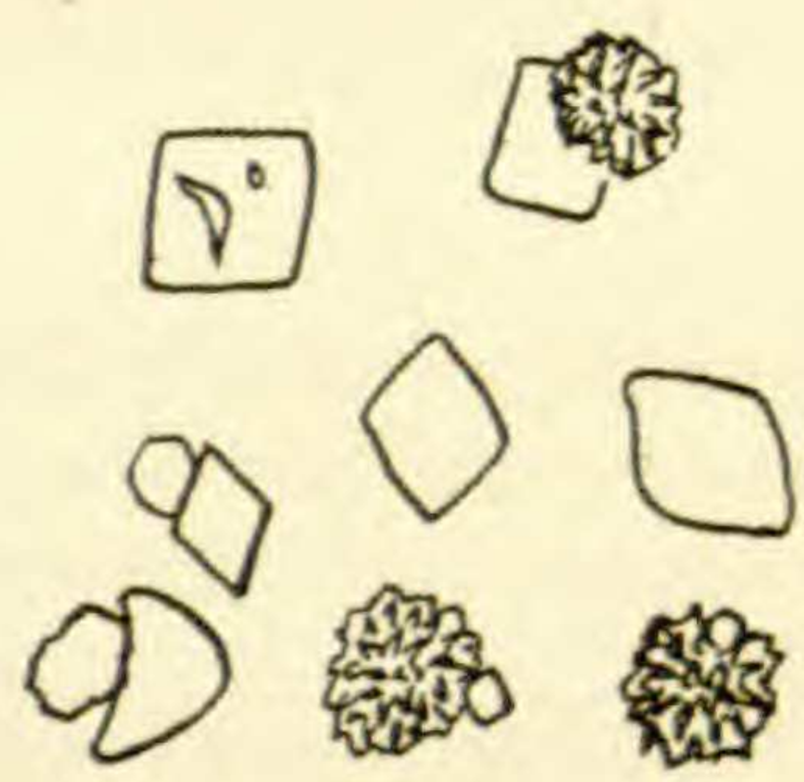

FIG. 4

FIGS. 1–4.—Fig. 1, part of transverse section (diagrammatic) across node of wheat stem, showing position of statenchyma: heavily dotted line, amylostatenchyma; lightly dotted line, crystal statenchyma; ×20; fig. 2, portion of fig. 1 enlarged to show structure; ×70; fig. 3, portion of crystal statenchyma in longitudinal section; ×140; fig. 4, various forms of crystal statoliths; ×620.

statolith, for the usual starch grain, which is required as nutriment for the ear. If this be true for grasses in general, it may be one of the many subtleties of structure that have contributed to the extraordinary success of the group. I am not without hope that future work may not only establish the nodes of the wheat plant as sense organs, but may even show that they have some bearing, even if remote, on such a practical problem as the lodging of crops.

Summary

1. The wheat haulm possesses two types of statocyte: (1) the smaller containing movable starch grains, (2) the larger with one movable crystal of calcium oxalate. Both occur only in the nodes.

2. The rate of fall of the crystal is much greater, and the period of migration considerably less than the corresponding quantities for the starch grains.

3. It is suggested that the nodes of the wheat are definite sense organs, showing a high degree of evolutionary development, and that future study of the reaction to gravity of the plant should take them into account.

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